
TOWARD AN INTEGRATION OF EVOLUTIONARY ECOLOGY AND ECONOMIC BOTANY: PERSONAL PERSPECTIVES ON PLANT/PEOPLE INTERACTIONS¹

Jan Salick²

ABSTRACT

Plant/animal interaction is a well developed field of investigation in evolutionary ecology. Plant/people interactions have been less fully explored, yet warrant parallel investigation, incorporating ecological genetics, population ecology, chemical ecology, and community and landscape ecology. To illustrate the ways in which people and plants interact and how these affect their coevolution, I use my research on: wild and domesticated cassava (*Manihot* spp., Euphorbiaceae); wild and semidomesticated cocona (*Solanum sessiliflorum*, Solanaceae); Amuesha farming and forestry systems; campesino and natural forest management of non-timber forest products in the Rio San Juan basin, including population studies of ipecac (*Cephaelis ipecacuanha*, Rubiaceae); and conservation, from germplasm conservation to landscape planning. Interrelating socioeconomic and biophysical research—the reciprocal people/plant perspectives—needs further development.

Plant/animal interactions have been studied extensively within the framework of evolutionary ecology (Ehrlich & Raven, 1964, 1967). An elaborate body of theory, methodology, analysis, data, and interpretation has been developed incorporating ecological genetics (Ford, 1964), population ecology (Begon & Mortimer, 1981), chemical ecology (Rosenthal & Janzen, 1979), community and ecosystems ecology (Whittaker, 1975), and more recently landscape ecology and global change.

Still, evolutionary ecological investigation of plant and animal interactions needs to better integrate people. Irrefutably, people affect plant populations and plant populations intensely affect people. This separation of people from animals in evolutionary theory dates back at least to Darwin. Although, using domesticated animals extensively to document evolution (Darwin, 1868), Darwin habitually differentiated between natural selection and artificial selection.

In evolutionary theory (Strickberger, 1968), the variety of mechanisms responsible for modifying

the reproductive success of a genotype is known as selection. Human knowledge of certain aspects of selection is prehistoric, including people's attempts to modify the plants and animals upon which they are dependent. Since the reproductive success of these domesticated organisms is determined by people's conscious selection of the parents of each generation, this mechanism of selection was named artificial selection. By contrast, organisms whose reproductive success is not determined by human choice are considered to be subject to natural selection.

These are artificial distinctions within the same selection process, resting on a past conviction that human consciousness is something apart from nature. Does an orangutan rejecting a less tasty durian do so any less consciously than a person selecting a tasty one to plant? Consciousness aside, is an ant defending an acacia qualitatively different from a person laying fence or shooing crows? Are not people (from a plant's perspective) really herbivores and dispersal or defense agents, exerting

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² Present address: Jan Salick, Associate Professor, Department of Environmental and Plant Sciences, Ohio University, Athens, Ohio 45701, U.S.A. e-mail: Salick@ouvaxa.cats.ohiou.edu.



FIGURE 1. Cocona (*Solanum sessiliflorum* Dunal) is an underexploited tropical crop with (a, left) tomatolike fruits and (b, right) eggplantlike foliage.

selection pressures regardless of consciousness? Additionally, people's selection is not always conscious. We have not intended to select for resistant malaria. We have not intended to select for plant breeding systems (see below). But we have. Human selection is not artificial or unnatural.

From this perspective, economic botany is primed for a "new synthesis" (Fisher, 1930), for an integration of ecological and evolutionary economic botany. I have been exploring simple possibilities for the last ten years: basically, reinterpreting plant domestication, cultivation, and management as plant/people interactions.

PLANT DOMESTICATION: PEOPLE AFFECTING PLANT GENETICS

Plant domestication has been defined as the genetic alteration of plants brought about by the activities of people (Simpson & Conner-Ogorzaly, 1986). Such genetic alteration can be studied using the prescribed methods, analysis, interpretation, and theory of the new synthesis. These methods and analyses were the basis of a study of crop domestication and evolutionary ecology of Cocona

(*Solanum sessiliflorum* Dunal) (Salick, 1992c; see also Salick, 1990, 1992b; Salick & Merrick, 1990).

Cocona (Fig. 1) is an underexploited tropical crop (Vietmeyer, 1986). Rustically domesticated varieties co-occur with wild phenotypes. These cross and produce fertile offspring. People actively select among offspring for spineless varieties (consciously) and (less consciously) for fruit qualities: since indigenous people seldom plant cocona, but rather let effective human dispersal by ingestion do its task, fruit are selected by being eaten. In contrast, spiny cocona growing under cultivation are actively weeded out of future gene pools. In the wild, cocona are small fruited and spiny. Domestication is an ongoing process, appropriate for population genetic investigation.

Additionally, the genetics are amenable. Spines were found to be one-gene dominants, which readily function as field markers. In experimental gardens, gene flow was measured. In reciprocal transplant field experiments selection by people, other herbivores, and composite mortality factors were measured in gardens, pastures, and riverbanks, respectively. These variables are the basis for a Hardy-Weinberg model (Falconer, 1981) of co-

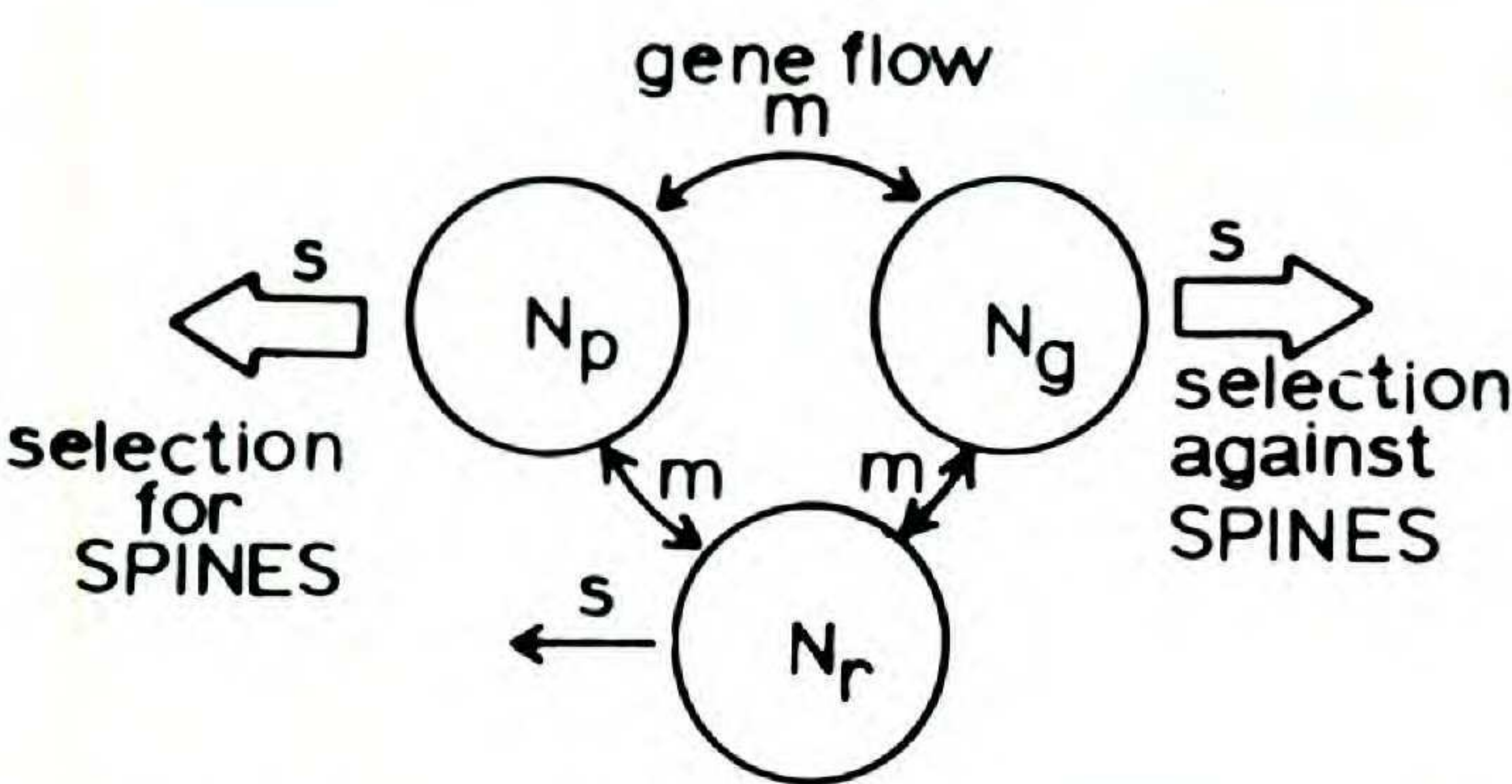


FIGURE 2. A simple Hardy-Weinberg model for cocona domestication based on population genetics of spines. There are three populations of cocona (N): in pastures (p), swidden gardens (g), and along riverbanks (r). A single gene for spines flows (m) among these populations, while selection (s) acts against spines in gardens and along riverbanks, and for spines in pastures. Selection is heavy in pastures and gardens, represented by large arrows dominating gene flow and allowing equilibrium well skewed toward the selected trait.

cona domestication (Fig. 2), the predictions of which were not significantly different from the results measured in field populations.

Nonetheless, upon testing the assumptions of the Hardy-Weinberg model, it was obvious that, as in so many *Solanum* species, cocona is highly inbred. The result in the model is to demonstrate tremen-

dous opportunity for genetic drift and allele fixation in field populations. Not only is this a complicating theoretical result, it is also somewhat difficult for the cocona conservationist. One cannot expect to sample populations of cocona to represent its biodiversity since nearly each plant is a population in itself.

The population genetics of cocona fruits and their domestication were strikingly different from those for spines in the same organism. Cocona fruit characters are mostly maternally inherited (Fig. 3). Fruits from controlled diallel crosses were like those of fruit from the maternal plant regardless of pollen from which they were fertilized.

In general, single parent inheritance, be it variously by sexual or cytoplasmic inheritance or by vegetative reproduction, is the rule in cultivated plants (Table 1). People must select (unconsciously) for plant breeding systems. Human selection would favor breeding systems that facilitate selection, domestication, and cultivation. People may select unintentionally but effectively for simple inheritance patterns. Cocona demonstrates simple inheritance by a single dominant gene (spines), inbreeding (the entire genome), and maternal genetic inheritance (fruit size and shape). Other crops have simple inheritance by apomixis, selfing, and vegetative

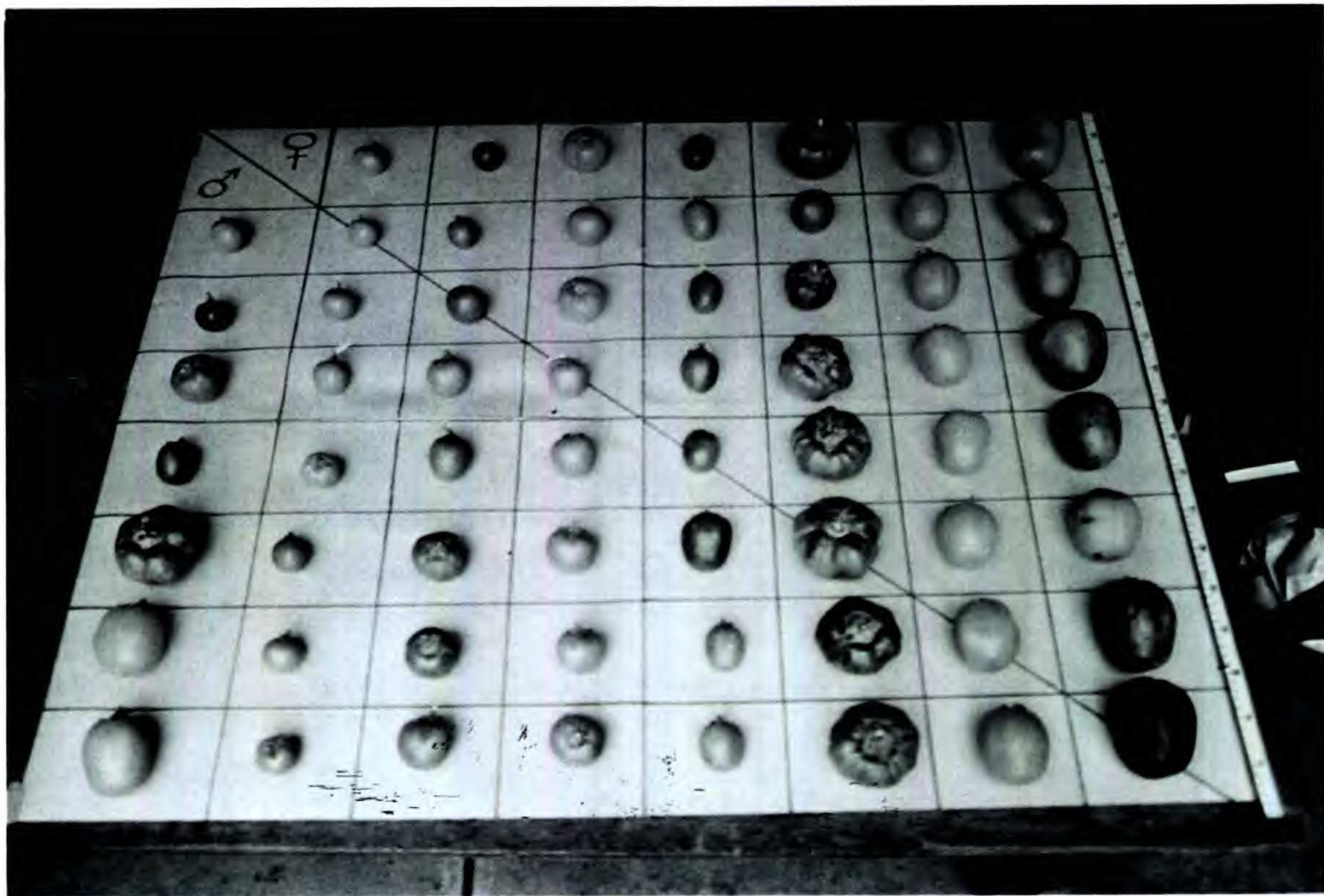


FIGURE 3. Cocona fruit characters are mostly maternally inherited as demonstrated by a complete diallel cross among seven varieties of cocona. All varieties were crossed with all varieties, including self-crosses marked by the diagonal line. Female parents are in the top row and male parents are in the left column. Progeny of any given female and male are found in the box corresponding to the column and row of its female and male parent, respectively. Parents and progeny are illustrated with representative fruit types. The significant result of the diallel is the overwhelming predominance of maternal inheritance for fruit characters.

TABLE 1. Types of uniparental inheritance in crops (both sexual and asexual). Uniparental inheritance has two main advantages: selection of desired characteristics is easy, and multiplication of the desired varieties is rapid.

True seed propagation	Vegetative propagation	Biotechnology
Selfing	Tubers	Meristem culture
Apomixis	Roots	Embryo culture
Autogamy	Cuttings	Rapid multiplication
Cytoplasmic inheritance	Stakes	Cloning
Mitochondrial DNA	Grafting	
Chloroplast DNA		

reproduction or, alternatively, may be reproduced through biotechnology (and have simple inheritance) by rapid multiplication. As our appreciation develops for the range and complexity of traits affected by natural selection, our vision of the effects of human selection and crop domestication likewise will expand.

PLANT CULTIVATION: PEOPLE AFFECTING PLANT POPULATION BIOLOGY

Plant cultivation has been defined as people “caring” for plants (Simpson & Conner-Ogorzaly,

1986). Caring ranges from minimal to intensive, from merely encouraging essentially wild individuals to careful planting and rearing of selected species. Cultivation and management can be differentiated, the former is related to plant species or populations, while the latter is plant community, system, or landscape oriented.

Cultivation can drastically affect plant population biology. Experiments documented changes in life histories, growth, production, and reproduction brought about by cultivation (Salick, in prep.). A plant species that grows in the wild and that is collected from the wild to cultivate was used in



FIGURE 4. Ipecac (*Cephaelis ipecacuanha*, Rubiaceae) is an understory tropical herb of economic importance because of its rhizomous production of alkaloids, which cause vomiting and can be used to avert poisoning. It is (a, left) collected from the wild or (b, right) rustically cultivated in forest or agroforestry beds.

these experiments, so that human selection toward domestication would be minimized. Additionally, given the previous results on the importance of direct inheritance, a plant species was selected that reproduces both sexually and vegetatively.

Ipecac (Fig. 4; *Cephaelis ipecacuanha* (Brot.) A. Rich., Rubiaceae) is an understory tropical herb of economic importance. Its roots are harvested for alkaloids that cause vomiting. The predominant alkaloid, emetine, is used to avert poisoning. It is collected from the wild or rustically cultivated in forest or agroforestry beds. Both in the wild and in cultivation it reproduces from seed and vegetatively. The experimental questions are, "How have people manipulated the population biology of this plant and why is it cultivated rather than merely collected or managed in the wild?"

Replicated, even-aged ipecac populations were grown in the tropical rainforest and under cultivation (Fig. 4) both from seed and from vegetative material. Vegetative reproduction from roots, stems, and growing tips was compared, although here data from seed and vegetatively sprouting roots are considered. The report on the two year data set on ipecac is still in press, but some clear trends can be summarized.

Plant height is greatest with vegetative cultivation (20 ± 5 cm), compared to sexual cultivation (11 ± 3 cm) and to vegetative reproduction in the wild (5 ± 2 cm). (Mortality was so high in sexually reproducing populations in the wild that no mature plant data are available.) Mean leaf area per plant differed greatly: 710 cm^2 with vegetative cultivation, compared to 110 cm^2 with sexual cultivation, and to 6 cm^2 for vegetative reproduction in the wild. Total plant biomass and root yield was greatest for vegetatively reproduced plants under cultivation (53.2 ± 15.2 g and 26.7 ± 6 g, respectively) compared to sexually reproduced plants under cultivation (25.7 ± 6.1 g and 18.6 ± 4.7 g), and vegetatively reproduced plants in the wild (3.5 ± 1.5 g and 2.5 ± 0.8 g). Flowering plants were only found among those vegetatively cultivated ($75\% \pm 8$). Death rate was highest among sexually reproducing plants in the wild (86% in the first year and 100% in the second year), compared to sexually reproducing plants under cultivation (66% year 1, 30% year 2), and vegetatively reproducing plants in the wild (43% year 1, 34% year 2) and vegetatively reproducing plants under cultivation (17% year 1, 25% year 2).

Thus, cultivation by vegetative reproduction increases ipecac plant growth, production, and reproduction and reduces mortality. Population ecology provides methodologies to address economic botany inquiry into these basic processes.

PLANT MANAGEMENT: PEOPLE AFFECTING PLANT COMMUNITIES AND LANDSCAPES

My work with plant management techniques and results deals with both agricultural and forestry management, their interactions, and to a lesser degree a larger landscape management. I have concentrated on both indigenous and campesino management techniques and more formal, technical methods of plant husbandry (and wifery—see gender in Amuesha agriculture, below).

Much attention has been given to intercropping and diverse host plant communities as a defense against insect herbivores (Risch et al., 1983). As evolutionary ecology might predict, some insect populations are adapted to such spatial diversity, however, and respond to other variables, for example, temporal diversity. Such turned out to be the case with cassava and the cassava lacebug.

Cassava (*Manihot esculenta* Crantz, Euphorbiaceae) is the traditional lowland Amazonian staple starch crop. It is grown throughout much of tropical Latin America and Africa as well as Asia below an elevation of approximately 2000 m. Traditional agroecological management of cassava often involves intercropping (Salick, 1983a, 1989a, b; Salick & Merrick, 1990). Wild cassava (*Manihot* spp.) also grows in diverse communities (Salick, 1983b; Salick & Merrick, 1990). Cassava lacebug is an herbivore adapted to this spatial diversity. My studies confirm that the herbivore is more abundant on cassava growing in diverse communities.

In contrast, temporal diversity achieved through crop rotation thwarts the poorly dispersing cassava lacebug. Wild cassava is perennial, while domesticated cassava is usually grown as an annual. Cassava lacebug is a pest on the perennial but is not adapted to annual relocation. When cultivated cassava is grown continuously, planted year after year in the same field and thus simulating a perennial host, cassava lacebug thrives; while annual cassava managed in rotation with other crops (temporal diversity) defeats the herbivore. Such rotations characterize indigenous management of the annual cassava (see below, Salick 1989a, b; Salick & Merrick, 1990).

Cassava also provides a clear example of a reciprocal human adaptation to a chemical plant defense system. Cassava with variable cyanide and tannin contents is amenable to chemical ecological analysis (Salick, 1983a). The human interactions within this chemical ecology are intriguing since people have not only selected cassava with low defensive chemical contents ("sweet" varieties), but also have maintained the defensive chemicals



FIGURE 5. Plant community management is characteristic of indigenous agriculture. Agroecological management by the Amuesha of the Peruvian upper Amazon includes systems adapted and timed to extremely high rainfall patterns, and differing with soils.

in “bitter” varieties, evolving human behavioral mechanisms to extract these chemicals before use (processing bitter cassava is well described by Roosevelt, 1980). To develop studies on plant/people interactions more such reciprocal cases must be documented.

Plant community management is characteristic of indigenous agriculture (Fig. 5). The Amuesha (or Yaneshas) of the Peruvian upper Amazon (Salick, 1989a, b; Salick & Lundberg, 1990; Salick & Merrick, 1990) have agroecological systems adapted and timed to extremely high rainfall patterns, and differing with soils of seasonally flooded beaches, alluvial floodplains, and acid terraces and hills (Fig. 6). Additional systems are found on continually cropped lands and in permanent home gardens. Intercropping and staggered rotations are ubiquitous within cropping systems. High, alluvial floodplains, for example, are planted with maize followed by cassava in transition to plantains. Perennials are relayed into annual crops forming agroforestry systems: fruit trees are planted under plantains and left uncut in the ensuing utilized and lightly managed fallow. All of these stages include a great variety of interplanted, minor crops. An extended Amuesha family cultivates simultaneously various fields at several stages using different cropping and even forest management systems (see

below). In this way, plant community management takes on a larger landscape aspect, particularly when extended families interact and plan within an indigenous community.

Plant community management is characteristic also of natural forest management (Matthews, 1989), forest management for nontimber forest products, and indigenous and campesino forest management (Salick, 1992 a, d, f; Salick & Offen, 1992). As indigenous agriculture can be contrasted with modern monoculture (Salick & Merrick, 1990), so too can these traditional forms of forest management be contrasted with plantation forestry or with monospecific market development of nontimber forest products (Clay, 1992). Local peoples conserve and manage a diversity of forests for a diversity of products (Salick, 1992a, d, f; Salick & Offen, 1992), using a diversity of management techniques including indicator species, inplanting, transplanting, weeding, cultivating the soil, mulching, selective cutting, and liberation of desired species (Salick 1992d, f). Diversity is the mark of indigenous and traditional plant community management.

Again, plant community management can take on a larger landscape aspect with natural forest management. This may occur when indigenous or campesino families interact within a community

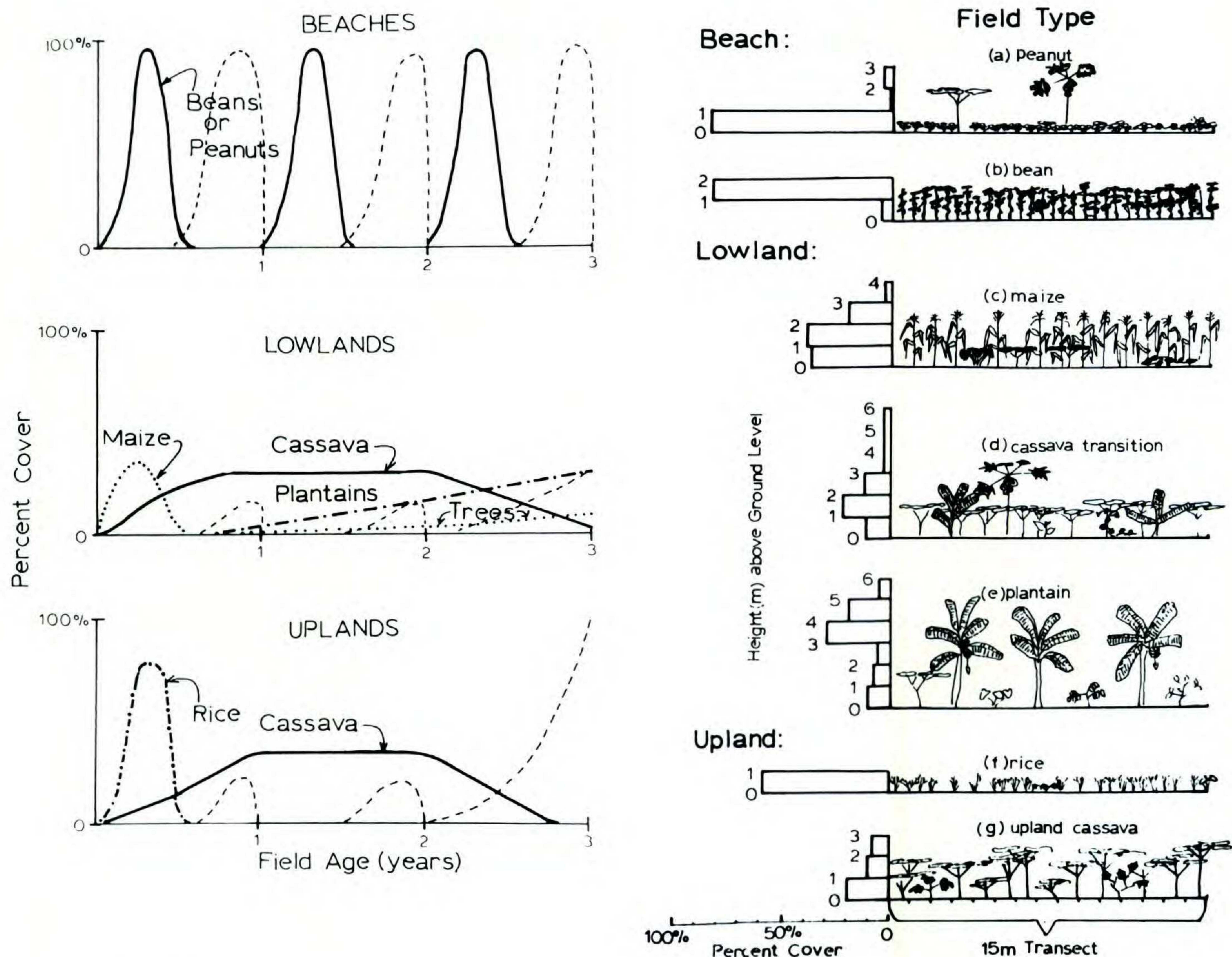


FIGURE 6. Topics in community ecology are very relevant to the sampling and analysis of traditional agriculture. (a, left) A three year time series analysis of Amuesha agricultural fields on three land types: seasonally flooded beaches, alluvial floodplains (lowlands), and acid terraces and hills (uplands). Fallows are marked with dashes (---). Only dominant crops are labeled although minor crops are prevalently intercropped, especially in the lowlands. (b, right) Transects (15 m) of the six field types—three land types with sequential rotations as in (a)—with average percent cover at each height class.

planning framework, or when silvicultural forest management becomes a part of conservation or regional planning (Fig. 7; Salick, 1992d, f).

THE HUMAN SIDE OF PLANT/PEOPLE INTERACTIONS

Some plant/animal interactionists bound their field to include only cases where both plants act on animals and animals on plants (coevolution sensu Janzen, 1980). So far, cassava processing aside, I have concentrated on the effects that people have on plants rather than the reciprocal. People/plant perspectives diverge from evolutionary ecology; they need to be developed through collaboration with social scientists. Two examples illustrate this difference.

Although it was not difficult to analyze human ecological patterns in Amuesha indigenous agriculture (above and Salick, 1989a, b), interpreting

the immense variation and change in these patterns drew together interacting ecological and sociological variables (Salick & Lundberg, 1990). The reasons for the impressive variability in Amuesha agriculture included a range of sociological factors from complex family histories to simple differences of opinion. In particular, gender and marital status were outstanding in the analysis of Amuesha agriculture (Salick, 1985, 1992e). Often when there was an exception to a trend, or an outlying data point, it represented a single woman. Among the Amuesha, single women practice agriculture differently and opportunistically construct subsistence strategies differently than most tribal members.

Traditional systems for the extraction, marketing, and tenure of nontimber forest products based on exploitation do not favor sustainable management of tropical forests, and less, the people directly responsible for that management—the ex-

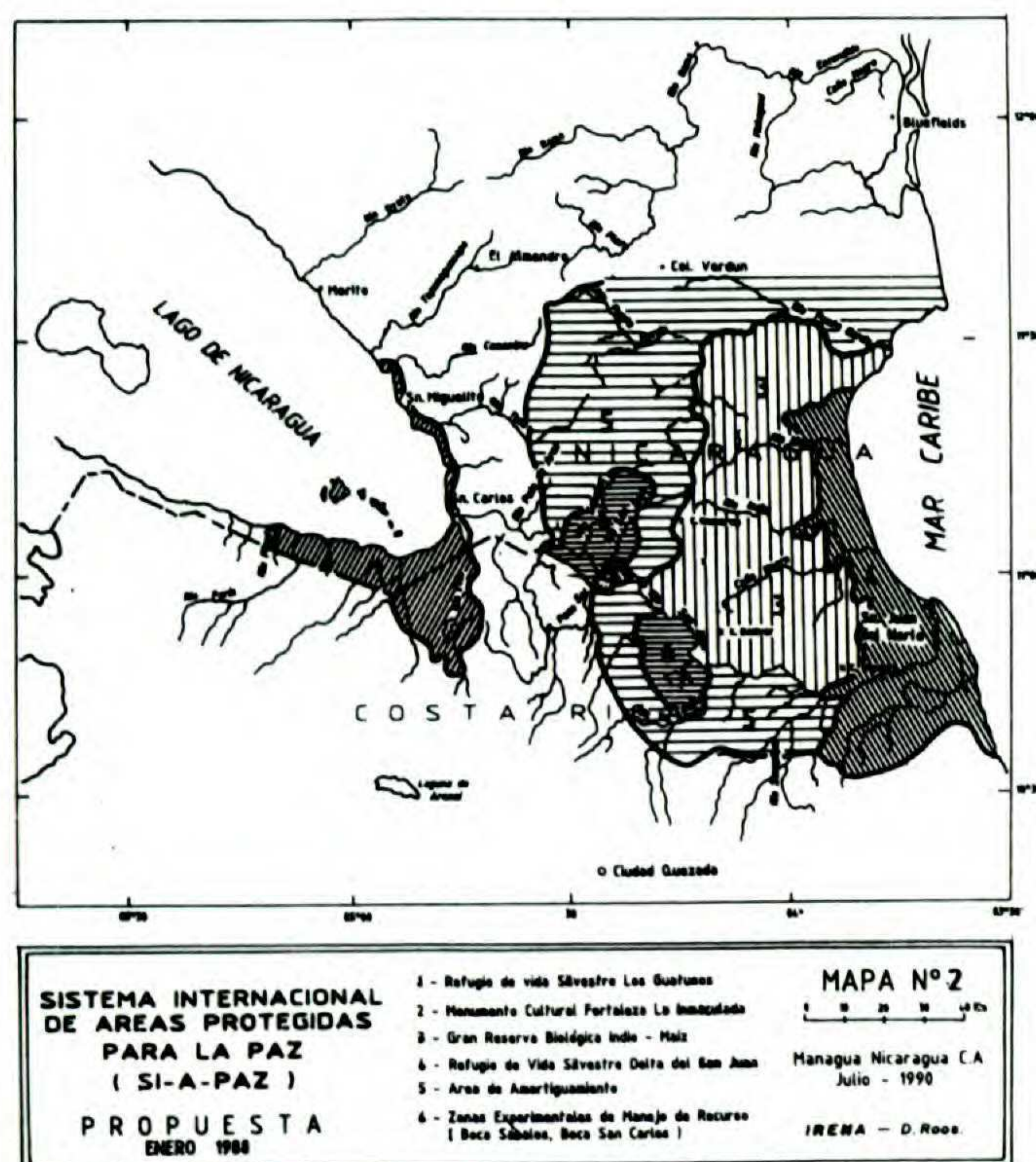


FIGURE 7. Plant community management can take on a larger landscape aspect, including natural forest management as a part of conservation or regional planning. In the International Peace Park (Si-a-Paz), Nicaragua and Costa Rica, the detailed park proposal includes (5) a buffer zone and (6) an experimental zone where our natural forest management experiments are located. (Map produced by IRENA.)

tractors. Further analysis (Salick, 1992d, f; Salick & Offen, 1992) uncovered additional confounding sociohistorical considerations, all well outside the purview of evolutionary ecology.

These attempts to develop economic botany from the human perspective are examples of the limits of evolutionary ecology in analyzing how plants affect people. Interdisciplinary collaboration seems the most productive line of investigation. Yet, the applications of evolutionary ecology to plant/people interactions have potential in determining how people affect plants.

CONCLUSION

Economic and ethnobotany interpreted as plant/people interactions can take advantage of many developments in evolutionary ecology. Within ecological genetics, people act toward plants as selective agents. Within population biology, plant life histories and their patterns of mortality, reproduction, and survival are greatly altered by people. Within chemical ecology, people both change and take advantage of plant chemical defenses for their benefit. Much of traditional plant management, both in agriculture and forestry, takes place at a plant community and landscape level. People ma-

nipulate many plant community variables that greatly affect plant evolutionary ecology. All of these areas of study have well developed methodologies, analyses, and theory, which can greatly enhance a synthetic economic botany. Undoubtedly, other subdisciplines within evolutionary ecology can yield equally productive integration.

LITERATURE CITED

- BEGON, M. & M. MORTIMER. 1981. *Population Ecology: A Unified Study of Animals and Plants*. Blackwell, Oxford.
- CLAY, J. 1992. Some general principles and strategies for developing markets in North America and Europe for nontimber forest products. Pp. 302-309 in M. Plotkin & L. Famolare (editors), *Sustainable Harvest and Marketing of Rain Forest Products*. Island Press, Washington.
- DARWIN, C. 1868. *Animals and Plants under Domestication*. London.
- EHRlich, P. R. & P. H. RAVEN. 1964. Butterflies and plants: A study in coevolution. *Evolution* 18: 586-608.
- & ———. 1967. Butterflies and plants. *Scientific American* 216: 104-113.
- FALCONER, D. S. 1981. *Introduction to Quantitative Genetics*. Longman, London.
- FISHER, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford Univ. Press, Oxford.
- FORD, E. B. 1964. *Ecological Genetics*. Wiley, New York.
- JANZEN, D. H. 1980. When is it coevolution? *Evolution* 34: 611-612.
- MATTHEWS, J. D. 1989. *Silvicultural Systems*. Oxford Science Publ., Oxford.
- RISCH, S. J., D. ANDOW & M. A. ALTIERI. 1983. Agroecosystem diversity and pest control: Data, tentative conclusions and new research directions. *Environm. Entomol.* 12: 625-629.
- ROOSEVELT, A. C. 1980. *Parmana: Prehistoric Maize and Manioc Subsistence along the Amazon and Orinoco*. Academic Press, New York.
- ROSENTHAL, G. A. & D. H. JANZEN (editors). 1979. *Herbivores: Their Interaction with Secondary Plant Metabolites*. Academic Press, New York.
- SALICK, J. 1983a. *Agroecology of the Cassava Lacebug*. Ph.D. Thesis, Cornell University, Ithaca, New York.
- . 1983b. Natural history of wild, crop-related species. *Proceedings of the Tall Timbers Conference. Environm. Managem.* 7: 85-90.
- . 1985. *Subsistencia y Mujeres Solas entre los Amuesha. Shupihui: Centro de Estudios Teológicos de la Amazonía, Iquitos*.
- . 1989a. Bases ecológicas de los sistemas agrícolas Amuesha. *Amazonía Indígena* 9: 3-16.
- . 1989b. Ecological basis of Amuesha agriculture. *Advances Econ. Bot.* 7: 189-212.
- . 1990. *Cocona (Solanum sessiliflorum): An overview of production and breeding potentials of an underexploited tropical crop*. Pp. 257-264 in G. E. Wickens et al. (editors), *New Crops for Food and Industry*. Chapman and Hall, London, England.
- . 1992a. Amuesha indigenous forest use and natural forest management. Pp. 305-332 in K. Red-

- ford & C. Padoch (editors), Conservation of Neotropical Forests: Working with Traditional Resource Use. Columbia Univ. Press, New York.
- . 1992b. Diversify your diet: Try some cocona cake, casserole, or creamsicles. *International Ag-Sieve*, Rodale 5: 6.
- . 1992c. Evolutionary biology of crop domestication: Maternal inheritance in *Solanum sessiliflorum*. *Evol. Biol.* 26: 247–285.
- . 1992d. Forest products and natural forest management within the Peace Park Buffer Zone, Nicaragua. Pp. 235–243 in F. R. Miller & K. L. Adam, Wise Management of Tropical Forests. Oxford Forest Inst., Oxford.
- . 1992e. Subsistence and the single woman among the Amuesha, Upper Peruvian Amazon. *Society and Natural Resources* 5: 37–51.
- . 1992f. The sustainable management of non-timber rain forest products in the Si-a-Paz Peace Park, Nicaragua. Pp. 118–124 in M. Plotkin & L. Famolare, Sustainable Harvest and Marketing of Rain Forest Products. Island Press, Washington, D.C.
- & M. LUNDBERG. 1990. Variation and change in Amuesha indigenous agricultural systems. *Advances Econ. Bot.* 8: 199–223.
- & L. MERRICK. 1990. Use and maintenance of genetic resources: Crops and their wild relatives. Pp. 517–548 in C. R. Carroll et al. (editors), *Agroecology*. McGraw-Hill, New York.
- & K. OFFEN. 1992. Influences of Market and Resource Tenure on Tropical Forest Management and Conservation in the Peace Park (Si-a-Paz), Nicaragua. *Etnobotánica '92*, Cordoba, Spain.
- SIMPSON, B. B. & M. CONNER-OGORZALY. 1986. *Economic Botany: Plants in Our World*. McGraw-Hill, New York.
- STRICKBERGER, M. W. 1968. *Genetics*. Macmillan, New York.
- VIETMEYER, N. D. 1986. Lesser-known plants of potential use in agriculture and forestry. *Science* 232: 1379–1384.
- WHITTAKER, R. H. 1975. *Communities and Ecosystems*. Macmillan, New York.